

SOME ASPECTS OF INTERRELATIONSHIPS AMONG THE DRYNARIOID FERNS*

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ABSTRACT

Morphological characters of 15 species belonging to seven genera of drynarioid ferns are presented and their significance relative to their origin, interrelationships, and trend of specialization discussed. Based on morpho-anatomical evidence accumulated, two morphological groups of drynarioid ferns are proposed: *Drynaria* and *Aglaiomorpha*. The attributes considered are: palea, rhizome; vegetative frond including epidermal cells, stomata, hypodermis, mesophyll, venation; fertile frond including sorus, sporangium, and spores; and gametophyte.

Existing knowledge of the formal taxonomy and phylogenetic trends among the drynarioid ferns are compared with this study and the different lines of descent are traced. It is suggested that the drynarioid ferns are probably diphyletic in origin and the trend of evolutionary progression has been towards reduction.

INTRODUCTION

The drynarioid group of ferns is an assemblage of large epiphytes of the Polypodiaceae regarded by most pteridologists as intimately related to each other. As currently understood, they consist of 8 genera (Copeland, 1947) and 37 species (Christensen: 1905–1906, 1917, 1934) throughout their range of distribution. *Drynaria* includes 20 species (Copeland, 1947; Holttum, 1954; Tindale, 1961) while the other genera are each represented by one or two species in the Indo-Malayan region. Several authors have expressed different opinions on the systematic position of the drynarioid ferns (Christensen, 1938; Ching, 1940; Holttum 1947, 1954; Copeland, 1947, 1960; Alston 1956; Pichi-Sermolli, 1958, 1959; Mehra, 1961; Nayar, 1970, 1974; Bierhorst, 1971; Wagner, 1973). Recently Crabbe *et al.* (1975) proposed a different classification in which drynarioid ferns were treated as a subfamily of Polypodiaceae without any further subdivision, while Ching (1978) gave the drynarioid ferns a formal status as a very natural and distinct family-Drynariaceae.

This group is quite different from most other polypodiaceous ferns and is considered as one of the most controversial with regard to their relationships and evolution. The views of Goebel (1928), Copeland (1929, 1947), Christensen (1938), Ching (1940), Holttum (1947, 1954), Nayar (1954, 1955, 1959, 1965), Nayar and Kachroo (1953), Zamora (1975), and Zamora and Vargas (1973 a, b) are varied and are highly susceptible to revision because they are based only on a limited number of species or on selected morphological characters. In view of the controversy regarding the relationship among the drynarioid ferns, the present investigation aims to explain the possible relationship among them and to discuss whether the splitting of the drynarioid ferns into two distinct morphological groups on the basis of morphological attributes is justifiable.

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MATERIALS AND METHODS

The present study is based on 15 species of drynarioid ferns (Table 1). Most of the materials used were collected from the fernery of the Natural Science Research Centre, University of the Philippines, Diliman, Quezon City except *D. fortunei*, *D. laurentii*, *D. propinqua*, *Pseudodrynaria*, and *Thayeria*, which were studied from herbarium specimens (Table 1).

Since the relationship and classification based on similarities and differences in one organ are unreliable unless supported by the totality of evidence from other parts of the plants, all possible morphological characters have been taken into account in this study. For the convenience of description, all the species are arranged in two morphological groups viz. *Drynaria* and *Aglaomorpha*. The *Aglaomorpha* group includes *Drynariopsis*, *Aglaomorpha*, *Merinthosorus*, *Pseudodrynaria*, and *Thayeria*, while the *Drynaria* group has *Drynaria* and *Photinopteris* (Chandra 1979 b, 1980).

TABLE 1. SPECIES STUDIED

Taxa	Source of Material
<i>Drynaria descensa</i> Copel.	U.P., NSRC, Fernery; P.M. Zamora, 73-0408 (PUH)
<i>D. fortunei</i> J. Sm.	S. Suzuki, PNH 63594; 63605
<i>D. laurentii</i> (Christ) Hieron	Jean Louis, PNH 29441
<i>D. propinqua</i> (J. Sm.) Wall.	Cavalerie, PNH 26053; Petelote, PNH 63596; B.K. Nayar, LWG, 74339
<i>D. quercifolia</i> (L.) J. Sm.	U.P. NSRC, Fernery; S. Chandra, 62(PUH)
<i>D. rigidula</i> (Sw.) Bedd.	U.P., NSRC Fernery; N.S. Vargas, 72-028 (PUH).
<i>D. sparsisora</i> (Desv.) Moore	U.P., NSRC, Fernery; S. Chandra, 16 (PUH)
<i>Photinopteris speciosa</i> (Willd.) Mort.	U.P., NSRC, Fernery; N.S. Vargas, 72-0186, (PUH).
<i>Drynariopsis heraclea</i> (Kunze) Ching	U.P., NSRC, Fernery, N.S. Vargas, 73-0449 (PUH)
<i>Pseudodrynaria coronans</i> (Wall.) Ching	S. Chandra, LWG, 94125; Poilana 1382 MICH; Y.W. Taam; 1861 MICH: Thakur Rup Chand; 3988 MICH.
<i>Aglaomorpha splendens</i> (J. Sm.) Copel.	U.P., NSRC, Fernery; S. Chandra, 48, 105 (PUH).
<i>A. meyeniana</i> Schott	U.P., NSRC, Fernery; S. Chandra, 109 (PUH).
<i>A. pilosa</i> (J. Sm.) Copel.	U.P., NSRC, Fernery; S. Chandra, 86 (PUH).
<i>Merinthosorus drynarioides</i> (Hook.) Copel.	D.F. Grether, PNH 3680; Grether and Wagner, PNH 3973.
<i>Thayeria cornucopia</i> Copel.	Edano, PNH 8770; Jacobs, PNH 10420.

OBSERVATIONS

Among the *Drynaria* group there appear to be two independent lines of evolution from the ancestor of the *Drynaria* group of species where one line gave rise to *Drynaria* and the other to *Photinopteris*. Contrary to the observations of Copeland (1947) and Nayar (1965), evolution appears to be in two directions from the *Drynaria* line (Fig. 2). One line gave rise to *D. rigidula* and the other to *D. quercifolia*, independently of one another.

D. rigidula is unique and is quite different from all other species of *Drynaria* in having: (1) rhizomes with undissected dorsal median vascular strands (as in *Photinopteris*), (2) stipitate pinnate fronds, (3) small foliar epidermal cells with shallow sinuous walls, (4) small stomata, (5) fewer number of areoles between main veins, (6) prominently impressed sori, (7) stellate paraphyses, and (8) small spores and sporangia. This possibly indicates that *D. rigidula* represents a line of evolution separate from that of other species of *Drynaria* but from the same common ancestor. This species, however, shows some similarities with *Photinopteris* in the following features: (1) undissected dorsal median vascular strand of the rhizome, (2) stipitate pinnate fronds, (3) two-ranked leaf arrangement, (4) small stomata, and (5) smaller sporangia and spores.

All other species of *Drynaria* have presumably evolved from *D. quercifolia* in two directions. One line gave rise to *D. sparsisora* and the other to all other *Drynaria* species. *D. sparsisora* exhibits relatively advanced features, viz. (1) thick coriaceous texture of the lamina with cartilaginous margins, (2) vestigial stipe articulation, (3) absence of xylem parenchyma between the tracheids in the meristeles of the rhizome, (4) slightly thickened upper foliar epidermis, (5) laminar hypodermis, (6) small stomata, (7) small upper foliar epidermal cells with shallow undulations, (8) small spores with spinulose exine ornamentation, (9) smaller sporangia (10) slightly reduced fertile fronds with minute sori, and (11) few elongated soral receptacles. This probably indicates that *D. sparsisora* is comparatively more advanced than *D. quercifolia* and has possibly evolved from it in a separate line. In contrast to Copeland (whose opinions of 1929 and 1947 are diagrammatically interpreted in fig. 1) this idea confirms the view of Holttum (1954) who considered *D. quercifolia* to be closer to *Drynariopsis* than to *D. sparsisora*. Comparative morphology of the sporophyte suggests that all other *Drynarias* are presumably evolved from *D. quercifolia*.

Among all *Drynaria* studied, *D. descensa* appears to be a reduced derivative of *D. quercifolia* which it resembles most (Copeland, 1960). *D. descensa* exhibits relatively advanced features viz. (1) small stature, (2) small nest leaves, (3) reduced xylem tissue (1-2 layers of tracheids) in the rhizome, (4) absence of xylem parenchyma between the tracheids in the meristeles of the rhizome, (5) paleae with shield-like bases and abruptly narrowed apices, (6) paleal margin with minute dentations, and (7) localized geographical distribution. This supports the contention that *D. descensa* is a reduced derivative of *D. quercifolia* and is therefore comparatively more advanced.

Photinopteris is similar to *Aglaomorpha* in the following features: (1) paleal morphology (*A. splendens*), (2) reduced fertile fronds, (3) development of coenosori, (4) verrucate areolate spores (*A. splendens* and *A. meyeniana*), and (5) small spores (*A. pilosa*).

Photinopteris is similar to *Drynariopsis* in the following features: (1) indistinctly clathrate paleae with (2) dentate margins, these (3) with glandular hairs, and (4) presence of foliar hypodermis and hydathodes. Though similar to *Aglaomorpha* and *Drynariopsis* in

some respects, *Photinopteris* differs from *Aglaomorpha* and *Drynariopsis* in such features as: (1) two-ranked leaf arrangement, (2) stipitate pinnate fronds (as in *D. rigidula*), (3) undissected dorsal median vascular strand of the rhizome (as in *D. rigidula*), (4) paleae with hairy, dentate margins, (5) club-shaped glandular hairs with waxy cap-like secretions, (6) large epidermal cells with deeply sinuous walls, and (7) low stomatal frequency.

Photinopteris is similar to the *Drynaria* group in the following features: (1) paleae with hairy, dentate margins and glandular marginal hairs with waxy cap-like secretions, (2) two alternate rows of fronds on the rhizome, (3) pinnate fronds (as in *D. rigidula*), (4) undissected dorsal median vascular strands of the rhizome (as in *D. rigidula*), (5) large foliar epidermal cells with deeply sinuous walls, and (6) low stomatal frequency. In view of the above, it is here suggested that *Photinopteris* be included in the *Drynaria* group.

Photinopteris, however, is comparatively more advanced than *Drynaria* in having: (1) long, wide-creeping rhizomes, (2) small stature with thick coriaceous fronds, (3) dimorphic fronds with reduced fertile laminae, (4) laminae with a hypodermis, hydathodes, and differentiated mesophyll, and (5) small spores with verrucate exine ornamentation. *Photinopteris* has, therefore, evolved separately from the ancestors of *Drynaria* and in a different line of evolution.

This combination of characters possibly indicates that *Photinopteris* is probably evolved independently of *Drynaria* but from the same common ancestor and that its similarities with *Drynaria* (especially with *D. rigidula*) are probably due to parallel evolution. *D. rigidula* probably branched off from the *Drynaria* line independently of the other *Drynaria* species. In contrast to Copeland (1947) and Nayar (1965), this view appears to support the earlier contention of Holttum (1954) who considered the origin of *Photinopteris* as being more uncertain and pointed out that its origin might have been through *Drynaria*, but in any case not immediately from *Drynariopsis* (Fig. 2)

In view of the two-ranked leaf arrangement characteristic of the *Drynaria* group, undissected dorsal median vascular strand of the rhizomes (as in *D. rigidula*), and stipitate pinnate fronds (as in *D. rigidula*), *Photinopteris* is included in the *Drynaria* group.

D. rigidula is quite different from all other species of *Drynaria* in having: (1) rhizomes with undissected dorsal median vascular strands, (2) sclerenchyma strands in the rhizomes, (3) stipitate pinnate fronds, (4) small stomata, (5) stellate foliar hairs, (6) prominently impressed sori, and (7) small sporangia and spores. This possibly indicates that *D. rigidula*, though similar to *D. quercifolia* in spore exine ornamentation, is probably nearer to it and branched off from the *Drynaria* line independently of other *Drynaria* species (Chandra & Zamora, 1979). Thus, *D. rigidula* represents a separate line of evolution from the same common ancestor. This combination of unique features in *D. rigidula* is possibly suggestive of the validity of its separation from *Drynaria* (it constitutes the section *Poronema* J. Sm.).

Among the *Aglaomorpha* group, *Drynariopsis* is considered as the most primitive genus. Thus, from *D. heraclea*, there have possibly evolved three genera of drynarioid ferns naturally similar in many respects, but strikingly different in other aspects. *Pseudodrynaria*, though similar to *Drynaria* in un-reduced fertile lamina and spinulose spores, differs from the *Drynaria* group in such features as: (1) one-ranked leaf arrangement, (2) broad humus-collecting leaf bases, (3) invaginated vascular cylinder of the rhizomes, (4) basally attached paleae with non-glandular apices and dentate margins, (5) presence of foliar hydathodes and a hypodermis, (6) elongated irregular coenosori, and (7) gametophytic trichomes. On the other hand, *Pseudodrynaria* is similar to the *Aglaomorpha*

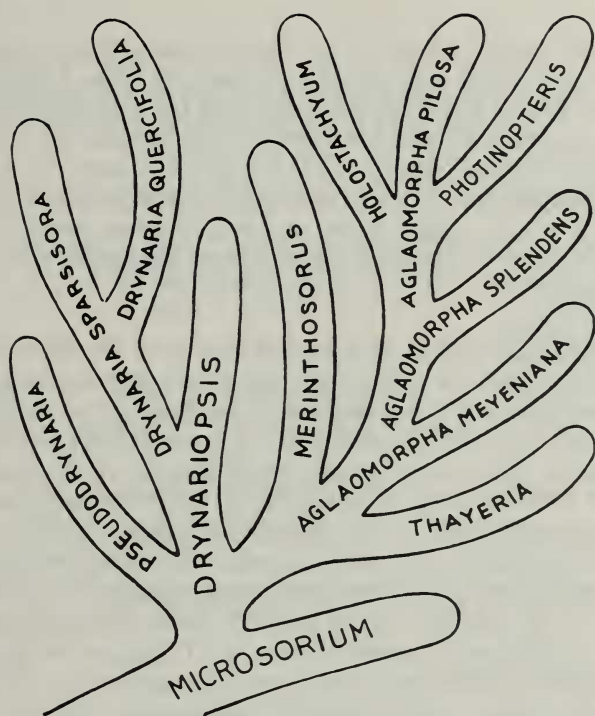


Fig. 1. A schematic representation of the inter-relationship of the drynarioid ferns (E. B. Copeland; 1929, 1947)

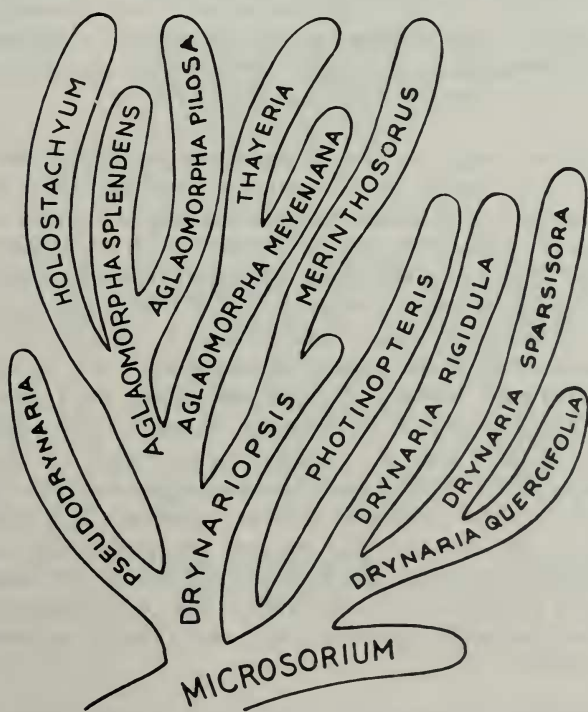


Fig. 2. A proposed schematic representation of the probable inter-relationship among the drynarioid ferns.

group in having: (1) uniform fronds with broad humus-collecting bases, (2) one-ranked leaf arrangement, (3) paleae with dentate margins, (4) foliar hydathodes and a hypodermis, (5) similar size of sporangia and spores, and (6) hairy gametophytes. *Pseudodrynaria* however, shows some advanced features over *Drynariopsis* viz. (1) tendency to form coenosori, (2) high stomatal frequency, (3) non-glandular apices of the paleae, (4) non-glandular paleal margins, and (5) spinulose spores. Thus, contrary to the observations of Nayar (1965), it is here suggested that probably *Pseudodrynaria* is more allied to the *Aglaomorpha* group and is possibly derived from *Drynariopsis* in a separate line of advancement (Fig. 2).

Another species presumed to have been derived from *Drynariopsis* is *Merinthosorus drynarioides*, which is regarded as more specialized than *Drynaria* because of the differentiation of its fronds into fertile and sterile portions. Based on gametophyte development, Nayar (1965) pointed out that *Merinthosorus* is not very close to any other drynarioid ferns, but its mature gametophyte is very much like that of *Drynaria*, *Pseudodrynaria*, and *Microsorium*. *Merinthosorus* however, differs from *Drynaria* and *Microsorium* in having: (1) one row of fronds on the rhizome, (2) basally attached paleae, (3) foliar hypodermis and hydathodes, (4) smaller stomata, (5) dimorphic fronds, (6) verrucate spores, and (7) small sporangia. *Merinthosorus* shows some similarities with *Aglaomorpha* (*A. meyeniana*) in having: (1) ribbon-shaped, basally attached paleae with similar dentations and without marginal glandular hairs, and (2) similar fertile fronds, spores, and gametophyte trichomes. These similarities appear to support the contention of Copeland (1947) that *Merinthosorus* is closely related to *Aglaomorpha* through *A. meyeniana* (Fig. 1). The similarity of gametophyte development of *Merinthosorus* (not found in any other drynarioid ferns) with that of *Drynariopsis* indicates that it is probably more intimately related to *Drynariopsis* than to any other drynarioid ferns and is possibly derived directly from *Drynariopsis* (Chandra, 1979a). Its similarities with *Aglaomorpha* are probably due to parallel evolution. The study of gametophyte development of *Drynariopsis* (Chandra 1979a) considerably strengthened the earlier view of Holttum (1954) who considers *Merinthosorus* to have been derived from *Drynariopsis* (Fig. 2).

Still another genus thought to have sprung from an ancestor like *Drynariopsis* is *Aglaomorpha*. Of the three species of *Aglaomorpha*, Copeland (1929, 1947) considered *A. meyeniana* as the source of *A. splendens* which in turn gave rise to *A. pilosa* (Fig. 1). *A. splendens* possesses comparatively primitive features such as: (1) indistinctly clathrate paleae with glandular apices, (2) large foliar epidermal cells with deeply sinuous walls, (3) large stomata, (4) low stomatal frequency, and (5) large sporangia and spores. *A. pilosa* is, however, comparatively more advanced than *A. splendens* in having: (1) long, wide-creeping rhizomes where each frond is associated with two branch buds, (2) high stomatal frequency, (3) small stomata, sporangia, and spores, (4) further reduced fertile fronds, and (5) localized distribution. Similarly, *A. meyeniana* also possesses some comparatively advanced features over *A. splendens* (i.e. absence of xylem parenchyma between the tracheids of the meristemes in the rhizome, further reduction of the fertile laminae, differentiated palisade, presence of upper and lower hypodermises, verrucate spores, and restricted distribution). This suggests the probability that *A. splendens* is the source of both *A. meyeniana* and *A. pilosa* and that *A. meyeniana* and *A. pilosa* evolved independently of each other in a different line of evolution from *A. splendens* (Fig. 2). Thus, the earlier view of Copeland (1929, 1947) that *A. meyeniana* is the source of *A. splendens* is refuted.

The genus *Thayeria* has presumably evolved from *A. meyeniana* (Figs. 1&2). Above the cornucopia base, the frond and fertile apex of *Thayeria* are like those of *A. meyeniana* to which it is most likely related (Copeland, 1929, 1947). Available information strongly

TABLE 2. CHARACTERISTIC FEATURES OF THE TWO GROUPS OF DRYNARIOID FERNS

Attributes	<i>Drynaria</i> Group	<i>Aglaomorpha</i> Group
1. Paleae structure	peltate, lanceolate or shield-shaped, marginal glandular hairs with cap-like waxy secretion	peltate or basally attached, lanceolate, shield-shaped, or ribbon-like; Marginal glandular hairs without cap-like waxy secretions
2. Frond arrangement	fronds in two alternating rows on the dorsal surface of the rhizome	fronds in one row on the dorsal surface of the rhizome
3. Nest leaves	present except in <i>Photinopteris</i>	absent as a rule
4. Foliage leaves	stipitate	sessile except in <i>Aglaomorpha pilosa</i>
5. Foliar hypodermis	absent except in <i>D. sparsisora</i> and <i>Photinopteris</i>	always present
6. Foliar epidermal cell size	large	smaller
7. Stomatal size	varies from $29\ \mu \times 38\ \mu$ to $42\ \mu \times 54\ \mu$	varies from $27\ \mu \times 32\ \mu$ to $34\ \mu \times 42\ \mu$
8. Stomatal frequency	varies from 38 to 79 per mm	varies from 59 to 140 per mm
9. Venation Pattern	finely reticulate, free included veinlets found only in a few areoles except in <i>Photinopteris</i>	broadly reticulate, free included veinlets present in all the areoles
10. Hydathodes	absent on the lamina surface except in <i>Photinopteris</i>	present as a rule
11. Nectary types	epicostular or hypocostular	always hypocostular
12. Leaf shape	fertile and sterile alike except in <i>Photinopteris</i>	fertile fronds more contracted than sterile ones except in <i>Drynariopsis</i> and <i>Pseudodrynaria</i>
13. Sori	usually punctiform throughout the frond except in <i>Photinopteris</i>	coenosoral or acrostichoid, only at the upper portion of frond except in <i>Drynariopsis</i> and <i>Pseudodrynaria</i>
14. Sporangial size	varies from $200\mu\text{--}400\mu \times 210\mu\text{--}380\ \mu$	varies from $200\text{--}240\ \mu \times 240\text{--}390\ \mu$
15. Spore size	varies from $26\text{--}43\ \mu \times 40\text{--}70\ \mu$	varies from $26\text{--}36\ \mu \times 42\text{--}56\ \mu$

indicates that *Thayeria* is the most advanced among the drynarioid ferns. Thus, dorsiventral creeping, scandent habit, and suppressed leaves on the dorsal surface of the rhizome appear to support the above contention and have finally strengthened earlier conclusions (Dickason, 1946; Holttum, 1964; Chandra, 1976) that dorsiventral creeping and a scandent habit is biologically specialized and is more probably a derived one. Other morphological attributes such as: (1) woody rhizomes, (2) paleae with closely spaced, broad, dentate margins, (3) lamina with adaxial and abaxial hypodermises, (4) smallest paleae with non-glandular apices, (5) smallest stomata, (6) highest stomatal frequency, (7) highly specialised humus-forming habit, and (8) reduced fertile portion, also support the above contention.

CONCLUSIONS

During the course of this study I have come across evidence indicating reduction in different parts of several species, i.e. stature, paleae, fronds, epidermal cells, epidermal cell wall undulations, stomata, sporangia, and spores. Thus, it is suggested that one evolutionary trend has been towards reduction. It appears that the *Aglaomorpha* group represents the advanced group among the drynarioid ferns, in particular *A. meyeniana*, *Merinthosorus*, and *Thayeria* (all of which possess thick adaxial foliar hypodermis and nearly similar fertile laminae) represent the most advanced species among the *Aglaomorpha* group (Chandra, 1979b).

From the foregoing facts it seems that these morphological attributes are of potential value and may be useful for the assessment of relative specialization and relationships among the drynarioid ferns.

On the basis of the accumulated evidence from comparative studies of the sporophytes and gametophytes, it is concluded that the contrasting combination of distinct characters among the drynarioid ferns supports the establishment of two natural, readily recognizable, and definable morphological groups namely *Aglaomorpha* and *Drynaria* (Table 2). It also indicates that the drynarioid ferns are probably diphyletic in origin, i.e. one line representing the *Drynaria* group and the other line representing the *Aglaomorpha* group.

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